RODENT SPECIES RICHNESS IS CORRELATED WITH CARNIVORE SPECIES RICHNESS IN SPAIN

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RÉSUMÉ. — *La richesse spécifique des rongeurs et celle des carnivores sont corrélées en Espagne*. — La diversité des niches écologiques favorise la coexistence des espèces, accroissant la richesse spécifique. La richesse spécifique des carnivores devrait donc croître avec celle de leurs proies, en raison des niches trophiques ainsi ouvertes. Cette hypothèse a été évaluée à l'aide de modèles linéaires généralisés utilisant des données de l'Espagne péninsulaire. Cinq facteurs susceptibles de générer une corrélation positive entre la richesse spécifique des carnivores et celle de leurs principales proies, les rongeurs, ont été contrôlés : le climat, l'activité humaine, l'autocorrélation spatiale, l'hétérogénéité de l'habitat et les effets du hasard. Les résultats montrent que la richesse spécifique des rongeurs et celle des carnivores sont positivement corrélées (r = 0,62) et que cette corrélation n'est due ni au climat, ni à l'activité humaine, ni à l'autocorrélation spatiale, ni à l'hétérogénéité de l'habitat. Ensemble, ces facteurs n'expliquent que 13,6 % de la variation de la richesse spécifique des carnivores alors que les rongeurs en expliquent 26,2 % (soit 50,4 % de la variance expliquée). De plus, la richesse spécifique des carnivores s'avère plus corrélée à celle des rongeurs qu'à celle de 28 autres taxons de vertébrés, la probabilité que ce soit le produit du hasard n'étant que de 0,034. En conclusion, cette étude met en évidence qu'une plus forte richesse spécifique des proies engendrerait une plus forte richesse spécifique des carnivores. La conservation de la densité des proies contribuerait ainsi à celle des carnivores.

SUMMARY. — The diversity of ecological niches favours species coexistence, increasing species richness. Therefore, carnivore species richness should increase with prey species richness, as this represents more trophic niches for carnivores. We evaluated this hypothesis with data from peninsular Spain, by using General Linear Models. We controlled for five alternative explanations for such a relationship: climate, human activity, spatial autocorrelation, habitat heterogeneity, and spurious chance, which might prompt a positive correlation between carnivore and rodent species richness (its main prey). Results show that rodent species richness was positively correlated with carnivore species richness (r = 0.62). The correlation between carnivore species richness and rodent species richness was not caused by climate, human activity, spatial autocorrelation or habitat heterogeneity. Together, these factors explained 13.6 % of variation in carnivore species richness, while rodent species richness alone explained 26.2 % of variation (50.4 % of explained variance). Moreover, carnivore species richness was more correlated with rodent species richness than with 28 other vertebrate taxa, with a probability of 0.034 of this being by chance. In conclusion, this study presents evidence that higher prey species richness may promote higher carnivore species richness. The conservation of prey diversity, thus, may contribute to the conservation of carnivores.

Niche segregation is a process that may favour the coexistence of species with similar ecological niches (Pianka, 2000). For this reason, sites with more ecological niches may contain more species (Huston, 1994; Chesson, 2000; Gaston & Blackburn, 2000; but see Kadmon &

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Allouche, 2007). Environmental heterogeneity may facilitate more diverse ecological niches, and, indeed, many studies have found that species richness increases with environmental heterogeneity, usually measured as diversity in land uses or habitat, or topographic variability (review in Tews *et al.*, 2004).

The ecological niche is determined by biotic as well as abiotic factors (Brown, 1995; Pulliam, 2000). Therefore, if different consumer species feed on different species (or functional groups of species), the higher the species richness is in a lower trophic level, the higher is species richness in the upper trophic level. For example, plant species richness favours species richness of phytophagous insects (Siemann *et al.*, 1998; Haddad *et al.*, 2001). At the same time, the higher the herbivorous insect diversity, the higher the predator insect diversity (Knops *et al.,* 1999). Greater plant species richness also promotes higher species richness of frugivores and, probably mediated by the trophic chain, insectivorous mammals (Andrews & O'Brien, 2000). *Ficus* species richness also encourages avian frugivore richness (Kissling *et al.,* 2007). Plant diversity is correlated with species richness of most of the vertebrates in different realms (Boone & Krohn, 2000; Pey-Yi & Rotenberry, 2005; Zhao *et al.,* 2006; Qian, 2007). On the other hand, other studies have failed to find a relationship between plant diversity and animal species richness when controlling for alternative variables such as climate, giving no support for the niche-segregation hypothesis (Hawkins & Porter, 2003; Hawkins & Pausas, 2004). This may be explained because, under determinate circumstances, a non-positive relationship between habitat heterogeneity and species richness is expected (Kadmon & Allouche, 2007).

Trophic-niche diversity may favour carnivore species coexistence (Ray & Sunquist, 2001). For carnivores, although prey overlap is relatively common, it is frequent for sympatric species to depredate different prey (Karanth & Sunquist, 2000; Ray & Sunquist, 2001; examples from Spain: Gil-Sánchez, 1998; Fedriani *et al.*, 1999; Padial *et al.,* 2002). For example, wildcats (*Felis sylvestris*) in Spain prefer to prey on rabbits (*Oryctolagus cuniculus*) than on rodents (Malo *et al.,* 2004); therefore, the presence of rabbits in a zone may relax the competition with other carnivore species more dependent on rodents, such as the stoat (*Mustela erminea*; e.g. Virgós *et al.,* 1999). In this framework, we predicted that higher prey species richness should favour higher carnivore species richness (hereafter, CSR). We tested this prediction with data from peninsular Spain, by examining the correlation between CSR and rodent species richness (hereafter, RSR).

Because this is a correlational study, causal explanations will be inferred (Brown, 1995). Nevertheless, if we find a positive correlation between RSR and CSR, to establish a direct causal relation would be speculative because other factors may mediate this correlation (e.g. Endler, 1995). To bolster the explanatory power of inferences, we tested for five alternative explanations for a correlation between RSR and CSR. (1) Climate might affect both RSR and CSR in the same direction, as zones with hotter or more productive climates harbour more species (Kerr & Packer, 1999; Waide *et al.*, 1999; Hawkins *et al.*, 2003; Evans *et al.*, 2005; Whittaker *et al.*, 2007); and this would promote an indirect positive correlation between RSR and CSR. (2) Human activity, having a negative effect on both RSR and CSR (e.g. Real *et al.,* 2003), also may provoke a positive correlation between both species richness, as species richness would be lower for both carnivores and prey in zones with higher human pressure. (3) As mentioned above, environmental heterogeneity promotes species richness (Tews *et al.*, 2004). If this factor favours RSR and CSR, a positive correlation for species richness between the two groups may emerge as a consequence. (4) Spatial autocorrelation might lead to a positive correlation between RSR and CSR, because, if there are many species of both carnivores and rodents in a square, there will also probably be many species from both groups in the adjacent squares (Legendre, 1993; ver Hoef & Cressie, 2001). (5) Species richness of different taxa are frequently correlated themselves although there is no causal relationship among them (Gaston, 2000; Wolters *et al.,* 2006).

MATERIAL AND METHODS

STUDY AREA

The study area was peninsular Spain (SW Europe, Fig. 1). Spain has a great variety of climates, though being primarily Mediterranean, with an oceanic climate in the Cantabrian region. Spain shows many environments, ranging from deserts to humid forests, mainly the consequence of the climatic gradient, but also because the Iberian Peninsula is very mountainous. The area was divided into 10×10 km squares (Fig. 1), which were the sampling units in the analyses. Overall, 5070 UTM squares were used, rejecting those without data available or with less than 100 km^2 (261 squares, 4.9 % of territory).

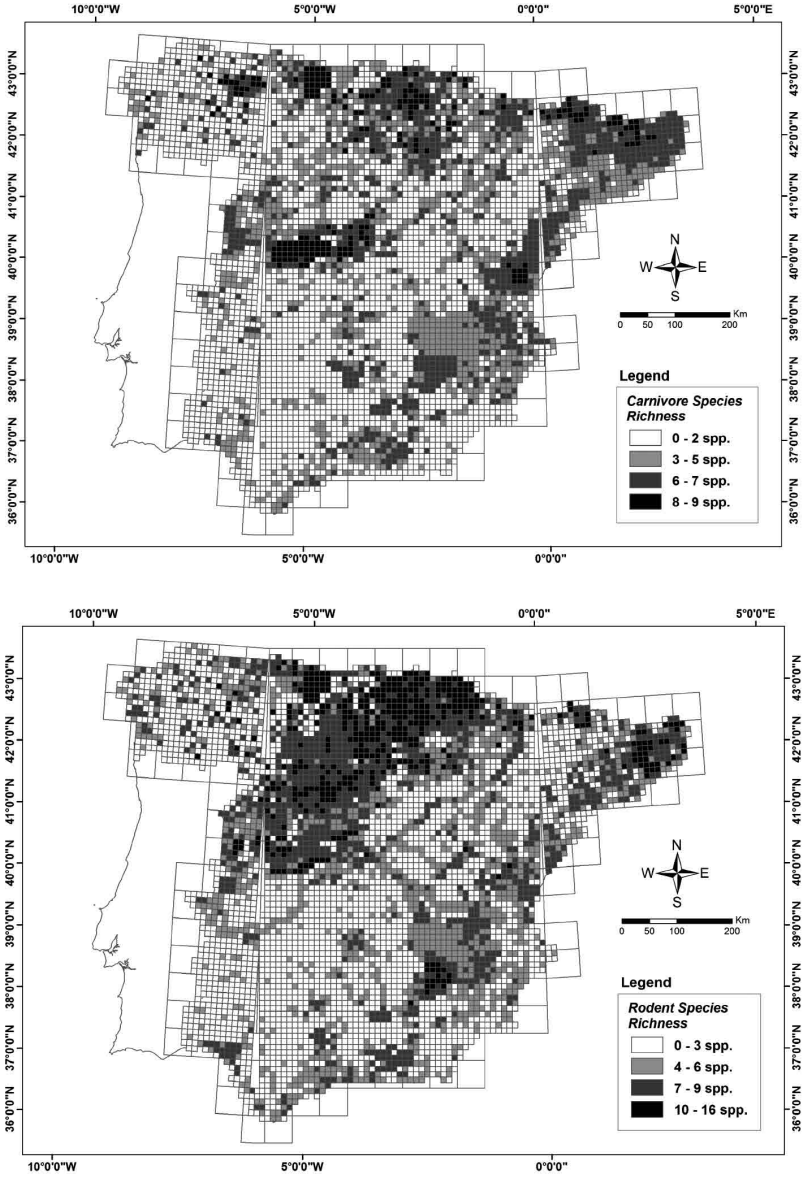

Figure 1. — Carnivore (upper map) and rodent (lower map) species richness per square in peninsular Spain. Grey tones refer to the abundance of species in each square.

PROCUREMENT OF VARIABLES

Carnivore species richness was considered as the number of species of the order Carnivora in each square. We used carnivores that depredate mainly rodents (n = 10; according to Wilson & Mittermeier, 2009; listed in Appendix 1), avoiding carnivores preying mainly on other sorts of prey (Wolf *Canis lupus*, Mongoose *Herpestes ichneumon*, Iberian Lynx *Lynx pardinus*, Bear *Ursus arctos*, Otter *Lutra lutra* and Badger *Meles meles*). The inclusion of these species in the analysis did not significantly alter the results (data available on request). Rodent species richness was considered to be the number of species of rodents (n = 21) in each square (Appendix 1). Both carnivore and rodent species richness were derived from the Vertebrate Dataset of Spain (Ministerio de Medio Ambiente, 2003; also see Palomo & Gisbert, 2002). Although this dataset probably has false negative (i.e., erroneous non-presence), it contains the best information available on mammal distribution in Spain.

To control for climate, we introduced into multivariate models the variables (1) mean annual temperature (in ºC), and (2) annual precipitation (in mm). In Spain, precipitation is strongly correlated with primary productivity (vegetation index; González-Taboada *et al.*, 2007). To control for human influence, we introduced (3) human population density (log-transformed), and (4) natural surface area (in km^2 per square; arcsin-transformed), as the surface covered by natural or naturalized land uses (forests, scrubland, pastureland and rocky land), excluding farmland and urban areas, as well as reservoirs and the sea. The natural surface area is a good indicator of the land transformation by humans, being the reverse of farmland area (Moreno-Rueda & Pizarro, 2007). To control for habitat diversity we introduced (5) altitude range (in m, a measure of topography variation), and (6) habitat richness, as the number of different land uses in each square (up to 45 different land uses; Appendix 2). Variables used in this study showed high levels of spatial autocorrelation, especially for distance below 100 km (Appendix 3). For this reason, in order to control for spatial autocorrelation, we introduced into the model the variables: longitude (Lon), latitude (Lat), Lon^2, Lat^3, $Lon^2 \times Lat$ and $Lon \times Lat^2$, according to Legendre (1993). We did not introduce the variables Lat^2, Lon^3 and Lon×Lat because they destabilized the matrix and least-squares could not be calculated. The introduction of these geographic terms into Ordinal Least Squares models allows account for the trend surface of the variables in the analysis, and decreases the possible effect of spatial autocorrelation on the results (Diniz-Filho *et al.,* 2003; Dormann *et al.*, 2007; Hawkins *et al.,* 2007). Moreover, in order to be sure that most of spatial autocorrelation was removed, we calculated the Moran's I of the residuals of the final model by using the SAM 3.0 program (Rangel *et al.*, 2006). Moran's I usually varies between -1 and 1, and high values are indicative of spatial autocorrelation (Diniz-Filho *et al.,* 2003).

All these variables (hereafter, alternative variables) were taken from the European Environment Agency (openly available in www.eea.europa.eu), by means of a geographic information system (SAGA; Conrad, 2005). Lastly, to examine whether the correlation between CSR and RSR is spurious, we correlated CSR with the species richness of 28 other different vertebrate taxa (listed in Table III). If the correlation between CSR and RSR is due to chance, then, the probability of being the highest is 1/29 = 0.034. Data on species richness for these taxa were taken from the Vertebrate Dataset of Spain (Ministerio de Medio Ambiente, 2003).

STATISTICAL ANALYSES

All variables in this study approximated a normal distribution, and they were standardized to mean 0 and standard deviation 1. First, we examined the correlation among all variables with Pearson's product-moment correlations. P-values were corrected by Bonferroni (Sokal & Rohlf, 1995). Insomuch as many predictors were correlated among themselves (Tab. I), we used General Linear Models (GLM) of multiple regressions (sum of squares type III), with the alternative variables (above) plus RSR as independent predictors of CSR. By so doing, we controlled for the four first alternative explanations discussed above for the correlation between RSR and CSR. Absolute values of correlations among independent variables were < 0.70, and tolerance was consistently > 0.30, implying that multicollinearity did not affect the results (Quinn & Keough, 2002).

To analyse the variance in carnivore species richness explained by RSR, in comparison with the other explanations, we partitioned the variance following Legendre (1993), considering four components of variance in CSR: (1) Var-rodent, variance exclusively due to RSR; (2) Var-alternative, variance exclusively due to the alternative explanations considered (climate, human influence, habitat heterogeneity, and spatial autocorrelation); (3) Var-common, variance due to the interrelationship among RSR and the alternative variables considered (simultaneously explained by both sets of variables); (4) Var-unexplained, variance not explained by RSR nor the alternative predictors considered. To calculate these variances, we performed different GLMs introducing only RSR (Rodent model), only the alternative variables (Alternative model), and all predictors (Full model), and by subtraction of variances: Var-rodent = Var(Full model) – Var(Alternative model); Var-alternative = Var(Full model) – Var(Rodent model); Var-common = Var(rodent + alternative) – Var(Full model); Var-unexplained = 1.0 – Var(Full model).

RESULTS

There were 2.71 ± SE = 0.03 carnivore species per square (considering the whole order Carnivora: 3.99 ± 0.04), with a coefficient of variation of 77.6 % and a range of 0-9 species per square. The correlation matrix (Tab. I) revealed that the variable rodent species richness (RSR) had the strongest correlation with carnivore species richness (CSR; r = 0.62). The rest of the variables were significantly correlated with CSR, except human population density, and most of them (except human population density and natural surface area) had a similar correlation

with RSR (Tabl. I). Therefore, the correlation between RSR and CSR might be mediated by these alternative variables.

To test this possibility, we performed a model with CSR as the dependent variable. The model showed that altitude range, habitat diversity, and natural surface area were positively and significantly correlated with CSR (Tab. II). Some spatial variables also affected CSR (Tab. II). However, rodent species richness remained the most important factor determining CSR ($F_{1, 5056} = 2762.9$; $\beta = 0.58$; Tab. II). The residuals of the final model showed no significant spatial autocorrelation, except for distance of 50 km, for which Moran's I was relatively low (0.15 ± 0.02), but significantly higher than zero (Fig. 2). Partitioning the variance in components (see Methods), the Rodent model explained 38.4 %, the Alternative model explained 25.8 %, and the Full model explained 52.0 % of variance. This implies that RSR alone was the most explicative variable for the carnivore species richness, explaining 26.2 % of the variance (50.4 % of explained variance), while 13.6 % were explained exclusively by the alternative variables (Var-alternative), and 12.2 % were explained by the relationship between rodent species richness and the other variables (Var-common). Therefore, rodent species richness was the primary determinant of carnivore species richness in Spain, even after controlling for the alternative explanations.

TABLE I

Matrix of correlations for the variables used in this study. Lon: longitude, Lat: latitude, Prec: precipitation, Temp: temperature, Pop: human population density, Nat: natural surface area, Hab: habitat diversity, Rang: altitude range, RSR: prey species richness, CSR: carnivore species richness. For more details, see Methods. In bold significant correlations after applying Bonferroni (K = 45; critical α = 0.001)

	Lat	Prec	Temp	Hab	Rang	Pop	Nat	RSR	CSR
Lon	**0.08**	**-0.21**	**-0.17**	**0.09**	**0.13**	**-0.05**	**0.05**	**0.14**	**0.33**
Lat		**0.48**	**-0.66**	**0.10**	**0.11**	**-0.12**	**0.14**	**0.33**	**0.25**
Prec			**-0.45**	**0.12**	**0.51**	**-0.12**	**0.20**	**0.14**	**0.16**
Temp				**-0.05**	**-0.37**	**0.50**	**-0.32**	**-0.26**	**-0.31**
Hab					**0.24**	**0.19**	**0.19**	**0.10**	**0.20**
Rang						**-0.17**	**0.44**	**0.06**	**0.30**
Pop							**-0.20**	**0.08**	-0.02
Nat								-0.01	**0.20**
RSR									**0.62**

TABLE II

Results of GLM with carnivore species richness as dependent variable. Multiple R = 0.72, $R^2 = 0.52$, $F_{14, 5055} = 395.8$, $p < 0.001$. β is the slope of the regression. In bold, significant effects after Bonferroni correction (K = 13; critical α = 0.0038)

	$F_{1, 5056}$	β	p
Rodent species richness	**2762.9**	**0.58**	**< 0.001**
Altitude range	**145.5**	**0.17**	**< 0.001**
Natural surface area	**91.4**	**0.12**	**< 0.001**
(Latitude)^3	**54.5**	**-2.08**	**< 0.001**
Latitude	**52.3**	**2.06**	**< 0.001**
Habitat diversity	**22.8**	**0.05**	**< 0.001**
Human population density	7.8	0.04	< 0.01
Mean temperature	4.9	-0.04	< 0.05
(Longitude)^2×Latitude	2.8	2.20	0.09
(Longitude)^2	2.7	-2.17	0.10
Precipitation	2.4	0.03	0.12
Longitude	2.0	0.83	0.16
Longitude×(Latitude)^2	1.3	-0.65	0.26
Intercept	734.3		< 0.001

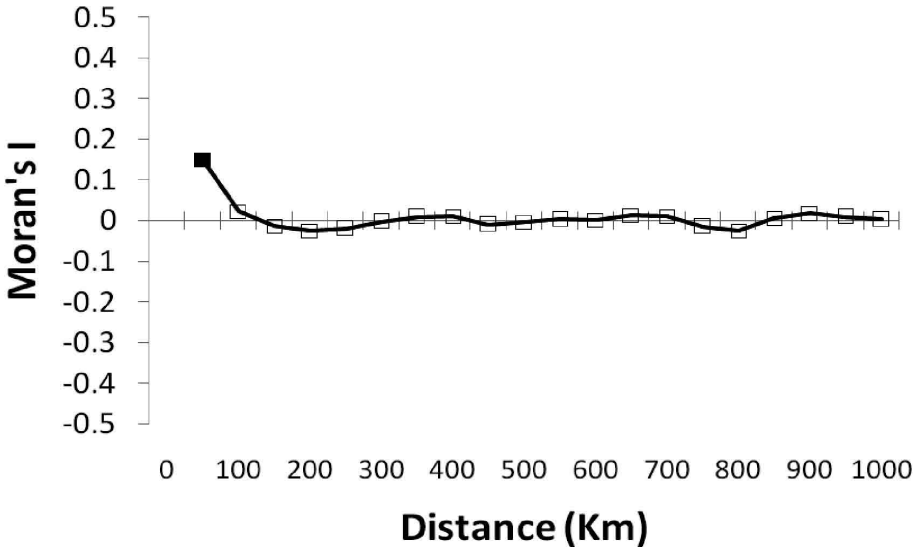

Figure 2. — Moran's *I* values for the residuals of the final model. Filled symbol indicates value that significantly differed from zero after Bonferroni correction ($K = 20$; critical $\alpha = 0.001$).

To ascertain whether the result found was spurious, we correlated CSR with the species richness of 28 other vertebrate orders and families (Tab. III). Rodent species richness had consistently the largest correlation with CSR. However, the correlation with insectivorous species richness was similar in magnitude ($r = 0.59$). This may be a consequence of RSR and insectivorous species richness being highly correlated ($r = 0.80$). When controlling for RSR, the correlations between CSR and insectivorous species richness decreased considerably ($r_{partial} = 0.21$; Tab. III, last column). If insectivorous species richness is included in the GLM, RSR remains as the main variable determining CSR ($F_{1, 5055} = 596.2$; $\beta = 0.41$), the effect of insectivorous species richness being almost half ($F_{1, 5055} = 187.9$; $\beta = 0.25$). The tolerance of the two variables with the model was 0.34 for RSR, and 0.29 for insectivorous species richness.

DISCUSSION

Results in this study support the hypothesis that more species richness of prey (rodents in this study) favours greater species richness of predators (carnivores in this study). We have controlled for alternative explanations that could mediate the correlation between rodent diversity and carnivore species richness: energy and productivity (i.e. climate; Hawkins *et al.,* 2003), human influence (e.g. Real *et al.,* 2003), habitat heterogeneity (i.e. habitat diversity and topography; Tews *et al.,* 2004), and spatial autocorrelation (Legendre, 1993). Together, these four explanations accounted for only 13.6 % of variation in CSR, while RSR explained 26.2 % of the variance (50.4 % of explained variance). However, 48 % of variation in carnivore species richness remained unexplained. Stochastic processes of extinction, non-considered variables, factorial or polynomial levels, sampling errors, and/or historical processes may account for this proportion of unexplained variance (e.g. Bustamante & Seoane, 2004; Wiens & Donoghe, 2004; He *et al.,* 2005).

Although sampling-effort bias is probably present in our data, we are confident that the results in this study were not a consequence of sampling bias for a number of reasons. First, sampling methods for carnivore and rodents differed, as carnivores were sampled mainly in the basis of road-killed specimens, while rodents were sampled mainly by trapping (this might

explain the high correlation between RSR and insectivorous species richness, as the two groups are sampled in a similar way). In addition, if some squares were more exhaustively sampled than others (for example, being more accessible to researchers, see Ferrer *et al.*, 2006), a spurious correlation between RSR and CSR would emerge. However, in this case, CSR would be also correlated with other vertebrate taxa. We analysed this by examining the correlation among CSR and species richness of other 28 vertebrate taxa. The correlation between CSR and RSR was the highest, the probability for this being simply by chance being 0.034. CSR was also heavily correlated with insectivorous species richness, but this was probably a sub-product of insectivorous species richness being strongly correlated with RSR. When controlling for RSR, the correlation between CSR and insectivorous species richness was considerably smaller. Moreover, sampling bias would reduce the explanatory power of models using this

TABLE III

*Correlations between carnivore species richness and 29 vertebrate taxa. The last column shows partial correlations after controlling for rodent species richness. In bold, significant correlations after applying the Bonferroni correction (k = 29; critical α = 0.0017). * Ungulates includes Artiodactyla and Perissodactyla*

	r	Partial *r*
Rodentia	**0.62**	
Insectivora	**0.59**	**0.21**
Lagomorpha	**0.51**	**0.36**
Ungulates*	**0.45**	**0.39**
Turdidae	**0.38**	**0.30**
Piciformes	**0.37**	**0.21**
Paridae	**0.35**	**0.24**
Motacillidae	**0.32**	**0.11**
Fringilidae	**0.31**	**0.23**
Emberizidae	**0.30**	**0.18**
Sylvidae	**0.28**	**0.14**
Falconiformes	**0.28**	**0.13**
Corvidae	**0.28**	**0.20**
Chiroptera	**0.26**	**0.05**
Ophidia	**0.25**	**0.19**
Sauria	**0.25**	**0.17**
Anura	**0.19**	**0.08**
Galliformes	**0.19**	**0.15**
Strigiformes	**0.18**	**0.09**
Urodela	**0.12**	0.01
Passeridae	**0.11**	0.03
Apodiformes	**0.10**	**0.10**
Hirundinidae	**0.09**	**0.11**
Columbiformes	**0.07**	0.04
Anseriformes	-0.02	**-0.07**
Alaudidae	-0.04	**-0.07**
Charadriiformes	**-0.07**	**-0.08**
Ralliformes	**-0.08**	**-0.14**
Ciconiiformes	**-0.08**	**-0.11**

dataset, and models performed with data of mammal distribution in Spain would be worse than models performed with, for example, bird species distribution (much better sampled). This did not occur, and models performed with mammal data do equally well with respect to models with other taxonomic groups that are better sampled (Moreno-Rueda & Pizarro, 2009).

Alternatively, higher CSR might favour higher RSR, for example, if CSR interrupts RSR throughout interspecific competition among prey species (Paine, 1966; Chesson, 2000). Similarly, Kissling *et al.* (2007) found that frugivorous bird species richness may favour fig richness. It is also possible that the higher the prey species diversity is, the higher the prey abundance is, and this latter factor directly affected carnivore species richness (Wright, 1983). Some studies have found that individual abundance and species richness are correlated (Haddad *et al.,* 2001; Hurlbert 2004; but see Currie *et al.* [2004] for a critical review). We could not test for this possibility, but in such case, it would be expected that the best competing carnivore species would increase its population density, displacing the other carnivore species, especially considering that intra-guild predation is frequent in carnivores (Palomares & Caro, 1999).

Some studies have shown the importance of habitat heterogeneity (habitat diversity or topography) for mammal species richness in general (Kerr & Packer, 1997) and carnivores in particular (Ruggiero & Kitzberger, 2004). The present study also shows the importance of habitat diversity and altitudinal range (habitat heterogeneity in general) for carnivore species richness in Spain. This relationship is assumed to be because environmental heterogeneity increases the diversity of ecological niches. Nevertheless, the most important component explaining CSR was RSR, which also increases the availability of ecological (diet) niches. The GLM showed that both variable sets independently affected CSR. Prey overlap is common in carnivores, although it is seldom complete (Gil-Sánchez, 1998; Fedriani *et al.*, 1999; Karanth & Sunquist, 2000; Ray & Sunquist, 2001; Padial *et al.*, 2002; Carvalho & Gomes, 2004; Barrientos & Virgós, 2006). Consequently, a niche segregation for prey and/or habitats in sympatry has been predicted in order to relax competition (Pianka, 2000), and several studies have found that competitive carnivores in sympatry show differences in the habitat use, which lead to dissimilarities in prey selection (review in Creel *et al.*, 2001). Therefore, it is possible that RSR reflects a variation in the number of available habitats not reflected in our variable "habitat diversity".

IMPLICATIONS FOR CARNIVORE CONSERVATION

Carnivores, being at the top of trophic chains, are especially prone to extinction (Terborgh, 1974; Purvis *et al.,* 2001; Woodroffe, 2001), and are frequently used to establish conservation priorities (Linnell *et al.,* 2000). We found that the natural surface area positively affected carnivore species richness, suggesting that carnivores are sensitive to landscape changes, as found in other studies (review in Sunquist & Sunquist, 2001). A number of studies suggest that CSR is sensitive to human disturbance (Real *et al.*, 2003; Virgós & Travaini, 2005). Nevertheless, we failed to find a negative correlation between CSR and human population density. However, at the scale used in this study, human population density is usually positively correlated with species richness (Pautasso, 2007). Therefore, the absence of a positive correlation between CSR and human population density is probably a consequence of the negative effects of human presence on carnivores. Similarly, Araújo (2003) found most vertebrate taxa in Europe to be positively correlated with human population density, with the exception of carnivore species richness. In contrast, rodent species richness did correlate positively with human population density. We found similar results in another study restricted to southern Spain (Table 6 in Moreno-Rueda & Pizarro, 2007).

Therefore, findings in the present study suggest that, in order to protect carnivores, it is important to conserve natural habitats, habitat heterogeneity and, especially, rodent diversity. The importance of prey conservation for carnivore conservation has been manifested for some particular species (for example, the Iberian Lynx *Lynx pardina*, Palomares *et al.*, 1995), but this study suggests that the conservation of rodents in general could be useful for the conservation of the entire group. The conservation of rodent habitats, in order to generate environmental diversity might relax competition among carnivore species, facilitating their coexistence.

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APPENDIX 1

List of rodents and carnivores present in peninsular Spain. All rodents were considered in the calculation of Rodent Species Richness, except those species recently introduced (e.g., coypu, *Myocastor coipus*). Only a number of carnivores were considered in the calculus of Carnivore Species Richness (indicated in the table), avoiding those which depredate mainly prey other than rodents (Iberian lynx, Egyptian mongoose : rabbits; wolf : ungulates; otter: fishes; badger: earthworms; bear: generalist). It is indicated the percentage of squares where each species is present (%), and its conservation concern (status) in Spain according to Palomo & Gisbert (2002; LC: Least Concern; DD: Deficient Data; NT: Near Threatened; VU: Vulnerable; EN: Endangered; CR: Critically Endangered; NE: No Evaluated).

Rodents	%	**status**	**Considered carnivores**	%	**status**
Apodemus flavicollis	2.7	LC	*Felis silvestris*	34.6	NT
Apodemus sylvaticus	60.1	LC	*Genetta genetta*	48.5	LC
Arvicola sapidus	30.6	VU	*Martes foina*	45.4	LC
Arvicola terrestris	4.2	LC	*Martes martes*	5.8	LC
Chionomys nivalis	3.6	NT	*Mustela erminea*	6.3	DD
Clethrionomys glareolus	7.2	LC	*Mustela lutreola*	3.1	EN
Eliomys quercinus	37.1	LC	*Mustela nivalis*	44.0	LC
Glis glis	4.3	LC	*Mustela putorius*	22.8	NT
Marmota marmota	1.4	NE	*Mustela vison*	7.5	NE
Microtus agrestis	16.9	LC	*Vulpes vulpes*	80.1	LC
Microtus arvalis	19.6	LC	**Non-considered carnivores**		
Microtus cabrerae	4.3	VU	*Canis lupus*	22.9	NT
Microtus duodecimcostatus	40.1	LC	*Herpestes ichneumon*	7.5	LC
Microtus gebei	3.5	LC	*Lutra lutra*	47.4	LC
Microtus lusitanicus	20.6	LC	*Lynx pardinus*	7.1	CR
Micromys minutus	3.3	LC	*Meles meles*	50.0	LC
Mus domesticus	79.7	LC	*Ursus arctos*	4.3	CR
Mus spretus	56.7	LC			
Rattus norvegicus	75.2	LC			
Rattus rattus	23.9	LC			
Sciurus vulgaris	33.0	LC			

APPENDIX 2

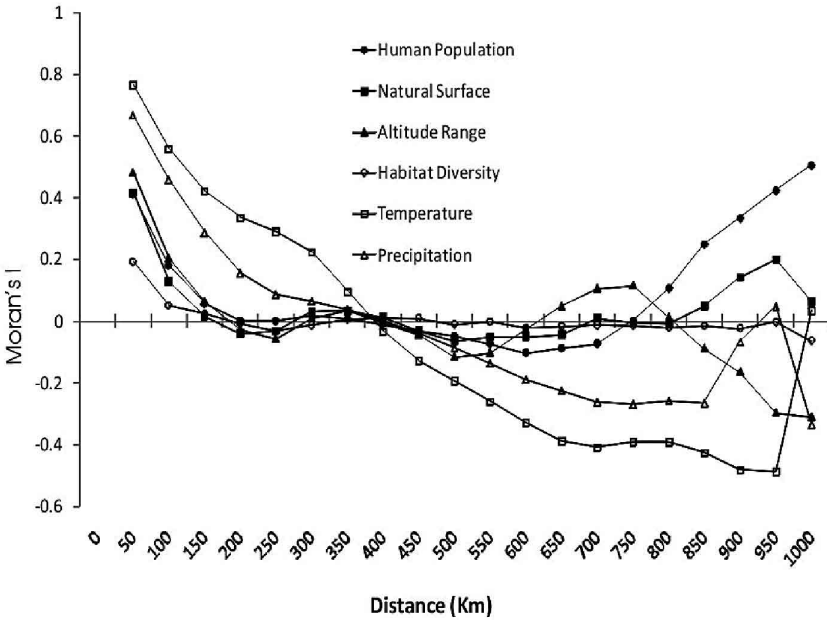
List of land uses employed in the study in the estimation of habitat diversity. Habitat diversity was considered as the sum of land use types present in each square. Data are available at European Environment Agency (www.eea.europa.eu).

Agro-forestry areas
Airports
Annual crops associated with permanent crops
Bare rocks
Beaches, dunes, sands
Broad-leaved forest
Burnt areas
Coastal lagoons
Complex cultivation patterns
Coniferous forest
Construction sites
Continuous urban fabric
Discontinuous urban fabric
Dump sites
Estuaries
Fruit trees and berry plantations
Glaciers and perpetual snow
Green urban areas
Industrial or commercial units
Inland marshes
Inland water bodies
Intertidal flats
Land principally occupied by agriculture, with significant areas of natural vegetation
Marine water bodies
Mineral extraction sites
Mixed forest
Moors and heathland
Natural grasslands
Non-irrigated arable land
Olive groves
Pastures
Peat bogs
Permanently irrigated land
Port and leisure facilities
Port areas
Rice fields
Road and rail networks and associated land
Salines
Salt marshes
Sclerophyllous vegetation
Sea and ocean
Sparsely vegetated areas
Transitional woodland-shrub
Vineyards
Water courses

APPENDIX 3

Moran's *I* values for the variables used in the study. (A) Environmental variables such as Human population density (filled circles), Natural surface area (filled squares), Altitude range (filled triangles), Number of habitats (open circles), Temperature (open squares), and Precipitation (open triangles). (B) Carnivore species richness (open circles) and Rodent species richness (filled squares).

(A)



(B)